



Analysis

Carbon Costs and Bushmeat Benefits of Hunting in Tropical Forests

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ABSTRACT

Unsustainable hunting is widespread globally, generating one of the primary threats to tropical vertebrates but providing important revenue for many people. Recent evidence suggests that by removing seed dispersing vertebrates, overhunting can induce shifts in tree species composition that reduce the amount of carbon stored in the forest. I developed a bioeconomic model to assess the conditions under which hunting might lead to the loss of forest carbon, and to compare the revenue lost via carbon erosion to that gained from bushmeat procurement. The potential long-term decline in forest biomass and the uncertain degree of ecological complementarity among frugivore species had the strongest influence on the amount of carbon lost via overhunting. Parameters related to frugivore population dynamics and the economics of the hunting system had relatively little influence. Total revenue in the system was maximized when hunter effort and the opportunity costs of hunting were low, suggesting that limiting hunting effort could maximize income for hunters by avoiding the depletion of both game species and potentially saleable carbon credits. These results highlight that enhanced understanding of long-term carbon responses to hunting in different tropical forests could help increase revenue for forest-dwelling people and contribute to global climate change mitigation efforts.

1. Introduction

Overhunting is nearly ubiquitous in tropical forests. Because many of the hunted animals are important dispersers of plant seeds (Redford, 1992), hunting-induced declines and outright extirpations of frugivores can have cascading impacts on plant recruitment (Brodie et al., 2009a). But while some plants might be negatively affected by loss of their seed dispersers, others (for example those with abiotic seed dispersal) may be unaffected by hunting, or even benefit via reduced competition with biotically dispersed species (Terborgh et al., 2008; Harrison et al., 2013). Hunting can therefore lead to shifts in the species composition of tropical tree assemblages (Terborgh et al., 2008; Harrison et al., 2013).

Recently it has emerged that the impacts of hunting could cascade ever farther -affecting not just tree populations and communities, but the forest ecosystem. In particular, because tropical tree species vary greatly in their size (Osuri et al., 2016) and the density of their wood (Chave et al., 2009), shifts in tree species composition in overhunted areas could alter the total biomass of the forest and therefore the amount of carbon that it stores. Simulations using demographic data from tree plots suggest that hunting could reduce forest carbon storage by 2–12% in Latin America and Africa (Osuri et al., 2016), potentially as high as 38% in portions of the Amazon Basin (Peres et al., 2016). Measurements of size and wood density in different tree age classes in Gabon indicated 15% declines in aboveground forest carbon in unsustainably hunted areas (Poulsen et al., 2013). Tropical forests store

huge amounts of carbon, so if these cascading impacts are representative of general patterns, the hunting of vertebrates in tropical rainforests could affect the global carbon cycle and hamper efforts to mitigate climate change (Brodie and Gibbs, 2009; Brodie, 2016).

However, our understanding of this potentially crucial issue is still very limited. Our knowledge about the ecological relationships between frugivorous vertebrates and tree community traits is in its infancy, limiting our ability to predict how much carbon might be lost from overhunting in different areas (Brodie, 2016). Moreover, the issue has never been placed in a bioeconomic context. A primary strategy by which the hunting-induced loss of forest carbon could be reduced would be for international programs such as REDD+ (Reduced Emissions from Deforestation and forest Degradation) to limit hunting (Brodie, 2016). But hunting provides important revenue to local people, either by providing products for sale in markets or by providing subsistence food that reduces the need to purchase or utilize other foods (Milner-Gulland and Bennett, 2003; Corlett, 2007; Harrison et al., 2016). So revenue that is potentially lost by hunting-induced erosion of forest carbon must be compared to the revenue gained by the hunting itself. But to date no studies have attempted to do this.

While it could be argued that sustainable hunting may be necessary for both forest carbon storage and long-term hunting yields, there are two important complications. First, because we know so little about how frugivore density affects tree community traits such as mean size or wood density (Brodie, 2016), we do not know whether hunting levels

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that were sustainable in terms of not driving the frugivores extinct were also able to maintain animal densities at levels sufficiently high enough to avoid significant erosion of forest carbon. Second, maintaining long-term hunting yields may or may not actually be in the economic best interests of the hunters. When the economic discount rate is relatively high, for example, the rational decision for hunters would be to harvest the animals to extinction quickly and invest the funds at a high rate of return (Clark, 1990; Ludwig, 2001).

Here I develop a bioeconomic model to compare the economic costs (via lost carbon) and benefits (via meat procurement) of hunting frugivores in tropical forests. I searched the published literature to find value ranges to parameterize the model. As discussed above, our understanding of much of the ecology and economics of the system is very poor. Therefore, rather than trying to generate exact predictions of costs and benefits, I assess the conditions under which revenue from carbon and hunting might outweigh each other, and ask where our (substantial) uncertainty in the various parameters most limits our predictive ability. In particular, I address the following objectives:

- 1) Determine the factors that influence how much carbon might be lost via overhunting.
- 2) Assess how we can maximize total revenue (from hunting plus forest carbon storage).

2. Methods

Most hunting in tropical forests is unsustainable, leading to depletion or extirpation of medium- and large-bodied animals (Milner-Gulland and Bennett, 2003; Harrison et al., 2016). When logging or road construction provide new access to previously remote areas, hunting can rapidly deplete vertebrate biomass (Robinson et al., 1999; Robinson and Bennett, 2000). I modeled the annual decline in the density (biomass) of large vertebrates ($\frac{dD}{dt}$, in kg y^{-1}) exposed to over-exploitation with a modified Gordon-Schaeffer function (modified by the inclusion of a θ shape parameter, as discussed below):

$$\frac{dD}{dt} = R_{frug} D_t \left(1 - \left[\frac{D_t}{D_0} \right]^\theta \right) - qED_t \quad (1)$$

where R_{frug} is the intrinsic rate of change in frugivore density in the absence of hunting or competition, D_t is frugivore density in year t (ranging from D_0 , the original biomass of medium- to large-sized frugivores in a given tropical forest ecosystem, to D_T , the final biomass after exploitation over a given time period T), q is the catchability coefficient of the frugivores, E is hunter effort, and θ is a shape parameter controlling the expression of density dependence in the frugivores (Sibly et al., 2005). See Table 1 for ranges of these (and other) parameter values. The product qE is the proportional exploitation rate of frugivores, making this model equivalent to the theta-logistic proportional harvest model (Ludwig, 2001).

I estimated the total income generated from hunting (in 2015 USD km^{-2}) over time period T as:

$$Income_{\text{hunting}} = \sum_{t=1}^T (qED_t)(\delta^{T-t})(P_{\text{bushmeat}}) \quad (2)$$

where P_{bushmeat} is in 2015 USD per kilogram and δ is the economic discount rate (Table 1). The costs of hunting were measured, following the Gordon-Schaeffer model, as the product of annual hunter effort (E) and per-unit-effort cost (a), discounted over time based on δ . Per-unit-effort costs were the opportunity costs of not engaging in paid employment (Table 1), standardized to a per-area unit (km^{-2}) based on human population densities in hunted tropical forests (Bennett and Robinson, 2000; Hill and Padwe, 2000; Robinson and Bennett, 2000). Hunting revenue ($Revenue_{\text{hunting}}$) was then $Income_{\text{hunting}}$ minus total costs.

The forest carbon remaining at time T (C_T ; t km^{-2}), as a function of declines in frugivore density, was estimated with a power function:

$$C_T = B_{\text{Forest}} - (B_{\text{Forest}} L_{\text{max}})(1 - F_T^z) \quad (3)$$

where B_{Forest} is the aboveground biomass of carbon in the forest in t km^{-2} , L_{max} is the maximum proportional loss (if any) of forest carbon if frugivores are completely removed from the system, F_T is the proportion of the original frugivore density still remaining at time T , and z is a shape parameter modeling frugivore complementarity. Declines in frugivore density could reduce forest carbon linearly ($z = 1$) if zoochorous tree regeneration depends strictly on the quantity of seeds dispersed and all frugivore species are equivalent in their dispersal services. At $0 < z < 1$, initial declines in frugivore density (i.e. when animals are still close to carrying capacity) would have less influence on forest carbon storage than do declines when frugivore density is already low because, for example, functional redundancy among species (Brodie et al., 2009b) is still present at high densities. Alternatively still, frugivore declines could have strong effects on carbon initially ($z > 1$) if the species that provide the most or the highest quality seed dispersal (e.g. the largest mammals) are driven extinct first, as is often the case in overhunted tropical forests (Brodie et al., 2009b; Peres et al., 2016).

The proportional change (if any; ΔC) of carbon from the forest due to hunting was then calculated by:

$$\Delta C = \frac{C_T - B_{\text{Forest}}}{B_{\text{Forest}}} \quad (4)$$

and the revenue loss, in 2015 USD km^{-2} , from any hunting-induced erosions of forest carbon storage was estimated as:

$$Revenue_{\text{carbon}} = [B_{\text{Forest}} - (B_{\text{Forest}} \times \Delta C)](P_{\text{carbon}}) \quad (5)$$

where P_{carbon} is in 2015 USD t^{-1} . I performed literature searches to assess the potential values for the parameters in the model (Table 1). Then, for each of 1 million model runs, I randomly drew parameter values from uniform distributions bounded by the extreme values (see Table 1).

To address the study objectives, I used multiple regressions to compare the relative influence of each of the parameters in Table 1 (independent variables) on two dependent variables: (1) the carbon lost from the system (ΔC ; Objective 1), and (2) the total revenue obtained from the system, or $Revenue_{\text{hunting}} + Revenue_{\text{carbon}}$ ($Revenue_{\text{total}}$; Objective 2). The randomly generated parameter values from the model runs were standardized to have means of 0 and variances of 1 so that their model coefficients could be directly compared. I also report the strength of the relationships (measured as R^2 values from univariate regressions) between each parameter and the two dependent variables (cf. Mills et al., 1999; Wisdom et al., 2000).

3. Results

For Objective 1, the carbon lost (if any) from the system via overhunting-induced shifts in tree species composition was most strongly related the maximum potential biomass change following complete extirpation of frugivores (L_{max} ; $\beta = -0.77$; Table 2). Functional compensation among frugivores (z) was also related, though less strongly ($\beta = -0.29$), to the amount of lost forest carbon. Parameters related to the population dynamics of frugivores in the face of hunting, including the intrinsic rate of increase (R_{frug} ; $\beta = -0.03$) and the unhunted density of frugivores (D_0 ; $\beta = -0.001$) had little or negligible relationship with forest carbon change. Likewise, parameters associated with the hunting system, including frugivore catchability (q ; $\beta = -0.06$), hunter effort (E ; $\beta = -0.11$), and the opportunity cost of hunting (a ; $\beta = 0.001$) had relatively weak influence on forest carbon change.

For Objective 2, hunter effort (E ; $\beta = -0.20$), the opportunity cost of hunting (a ; $\beta = -0.13$), and the price of bushmeat (P_{bushmeat} ; $\beta = 0.11$) had the strongest influence on the total revenue ($Revenue_{\text{hunting}} + Revenue_{\text{Carbon}}$) generated by the system (Table 2); revenue increased when hunter effort was low. Parameters that were

Table 1

Value ranges, explanations, and supporting information for the bioeconomic model parameters explored here.

Parameter	Explanation	Value range	Notes
B_{Forest}	Forest aboveground biomass (t km^{-2})	5000 to 37,200	From West et al. (2010).
T	Time period over which hunting-induced changes in forest carbon occur (years)	35 to 100	Rapid changes (~ 35 y) in forest carbon were observed by Poulsen et al. (2013) in forest regenerating from selective logging; unlogged systems will likely take longer for hunting to affect forest carbon storage (Brodie, 2016).
$P_{Bushmeat}$	Price of bushmeat (2015 USD)	0.25 to 6.90	Based on published literature (Carpaneto and Fusari, 2000, Apaza et al., 2002, Fa et al., 2002, Milner-Gulland and Clayton, 2002, Cowlishaw et al., 2005, Wilkie et al., 2005, Willcox and Nambu, 2007, Foerster et al., 2012, Golden et al., 2014).
P_{Carbon}	Price of carbon (2015 USD t^{-1})	2 to 100	From 2006 to 2016 the price of carbon futures ranged from ~ 2 to ~ 32 USD t^{-1} (http://www.investing.com/commodities/carbon-emissions-streaming-chart ; accessed 26 October 2016) but could go significantly higher if global cap-and-trade policies were implemented.
D_0	Maximum density of large hunted animals (kg km^{-2})	800 to 3100	From a review by Robinson and Bennett (2000) of seven sites in the Neotropics and Afrotropics.
R_{frug}	Intrinsic rate of increase of frugivore populations	0.01 to 0.1	Order of magnitude variation in possible mammal population growth rates.
θ	Shape parameter controlling the expression of density dependence	-1 to 10	From Sibly et al. (2005)
q	Catchability coefficient: the proportion of available frugivore density that can be harvested with 1 unit hunter effort	0.1 to 0.8	A range of possible values used in light of no direct estimates of this parameter.
E	Annual hunting effort	$\frac{R_{frug}}{2q}$ to $\frac{2R_{frug}}{q}$	In a proportional harvest model with logistic population growth, harvest is sustainable up to $qE = R_{max}$, while maximum sustainable yield is at $qE = R_{max}/2$ (Ludwig, 2001). Harvest in many tropical bushmeat systems is unsustainable (Milner-Gulland and Bennett, 2003, Harrison et al., 2016).
a	Cost per unit hunting effort	0 to 2710	Opportunity costs are zero for hunters with no employment or land to farm. The upper limit of annual opportunity costs per unit area was estimated as the product of human population density and annual minimum wage. Human density in tropical forests should not exceed 1 km^{-2} for hunting to be sustainable (Bennett and Robinson, 2000) and, where hunting is sustainable, human density is generally much lower (Hill and Padwe, 2000, Robinson and Bennett, 2000). Non-hunting employment at minimum wage in Brazil (the largest tropical country) earns $\$2710 \text{ person}^{-1} \text{ y}^{-1}$ (2015 USD; https://tradingeconomics.com ; accessed 5 Feb 2018).
δ	Economic discount rate of bushmeat (Price in year t /Price in year $t-1$)	1.0 to 1.1	Amount by which hunting revenues could increase with investment. A purely subsistence hunting system might have $\delta = 1$ while market-based hunting could generate investment opportunities ($\delta > 1$); in this case the upper limit corresponds to a $10\% \text{ y}^{-1}$ rate of return.
L_{max}	Maximum proportional loss of forest carbon with all frugivores removed	0 to 0.4	Frugivore removal has no apparent effect on forest carbon in some systems (Harrison et al., 2013, Osuri et al., 2016). Extrapolating from highly overhunted parts of Amazonia (Peres et al., 2016), in the absence of frugivores, B_{Forest} might decline by up to 38%.
z	Frugivore complementarity	0.01 to 100	The relationship between relative frugivore density and forest carbon is linear at $z = 1$, concave at $0 < z < 1$, and convex at $z > 1$ (see Methods for biological explanations of these parameter values).

Table 2Influence of the model parameters (defined in Table 1) on forest carbon change and the total revenue generated in the system from bushmeat procurement and avoided carbon loss. Parameter influence is assessed via standardized coefficients (β) from multiple linear regression models; univariate R^2 values also shown.

	Proportional carbon loss		Total revenue	
	β (SE)	R^2	β (SE)	R^2
B_{Forest}	0 (0.001)	0	-0.019 (0.001)	0
T	-0.044 (0.001)	0.002	-0.024 (0.001)	0.001
$P_{Bushmeat}$	0 (0.001)	0	0.111 (0.001)	0.012
P_{Carbon}	0 (0.001)	0	-0.025 (0.001)	0.001
δ	-0.001 (0.001)	0	-0.017 (0.001)	0
R_{frug}	-0.031 (0.001)	0.007	0.052 (0.001)	0.002
D_0	-0.001 (0.001)	0	0.07 (0.001)	0.005
θ	0.157 (0.001)	0.025	0.04 (0.001)	0.002
q	-0.062 (0.001)	0	0.014 (0.001)	0.016
E	-0.108 (0.001)	0.008	-0.197 (0.001)	0.032
a	0.001 (0.001)	0	-0.129 (0.001)	0.017
L_{max}	-0.769 (0.001)	0.591	-0.027 (0.001)	0.001
z	-0.286 (0.001)	0.082	-0.01 (0.001)	0

important to determining the amount of forest carbon loss had relatively little influence on total revenue: L_{max} ($\beta = -0.03$), B_{Forest} ($\beta = -0.02$), and z ($\beta = -0.01$).

4. Discussion

Bushmeat hunting is one of the most important threats to tropical vertebrates around the world (Milner-Gulland and Bennett, 2003; Harrison et al., 2016), provides an important source of revenue for many people (Robinson and Bennett, 2002; Knapp, 2012), and could potentially affect the global carbon cycle (Brodie and Gibbs, 2009). Assessing the bioeconomics of hunting is therefore critical, but has not previously been done in the context of forest carbon storage (Brodie, 2016).

The simulations and parameter explorations performed here suggest that response variables vary in the degree to which they are influenced by different environmental and economic factors. If we are primarily concerned with estimating whether and how hunting reduces forest carbon, it is critical to understand the maximum amount by which forest biomass can decline in overhunted forests. This has only been estimated in a few tropical areas, and the results are highly variable (Poulsen et al., 2013; Bello et al., 2015; Osuri et al., 2016; Peres et al., 2016) suggesting an important direction for continued research.

Frugivore complementarity also strongly influences carbon loss

from the system. This is one of the model parameters about which we know the least. Simulation studies and limited empirical evidence suggest that the relationship between frugivore density and forest carbon storage could be positive in some areas (Osuri et al., 2016; Peres et al., 2016) but not others (Harrison et al., 2013; Osuri et al., 2016). But whether the relationship – when positive – is linear or saturating remains unknown. Ecologists have long been interested in assessing species' ecological effectiveness (Soule et al., 2003; Soule et al., 2005; Estes et al., 2013). The results presented here suggest that understanding the density of frugivores required to support forest carbon storage is a particularly critical facet of ecological effectiveness, given the implications for global climate change mitigation.

Interestingly, most of the variables related to the population dynamics of the frugivores and the economics of the hunting system had little influence on how much carbon was lost from the system. This is fortunate, because we often have very little information on these factors. The maximum density of frugivores is a topic about which our knowledge is increasing (Robinson and Bennett, 2000; Robinson and Bennett, 2004; Peres and Palacios, 2007), but where substantial knowledge gaps remain. The rate of population decline of hunted frugivores is something we know less about, but this can sometimes be estimated by comparing measured extraction (e.g. Robinson and Bennett, 2000 and references therein) to intrinsic rates of increase as estimated from allometric body size equations (e.g. Cole, 1954). The shape parameter controlling frugivore density dependence did have some influence on forest carbon change. This is interesting because other simulation studies have suggested that this factor was not important to consider in assessing the extinction risk of overhunted tropical vertebrates (Granados and Brodie, 2016). Unfortunately, we know very little about the values of this parameter for most vertebrate species.

If, in contrast, our primary concern lies in optimizing total revenue (from the combination of hunting and forest carbon), different factors are important to consider. Revenue was negatively related to hunter effort and the opportunity costs of hunting and, unsurprisingly, positively related to the price of bushmeat. This suggests that limiting hunting would be an ecologically and economically beneficial management strategy – avoiding the depletion of game stocks and the reduction in forest carbon.

Other parameters in this bioeconomic model were consistently less important. Much has been written about the role of economic discount rates in the valuation and potential sustainability of animal harvest systems (e.g. Clark, 1973; Clark, 1990; Flaaten, 1991; Lande and Engen, 1994), but this factor did not have strong effects on forest carbon loss or the revenue generated by carbon storage and bushmeat harvest. Substantial effort has also gone into estimating aboveground forest biomass in different tropical systems (e.g. Gibbs et al., 2007; West et al., 2010; Taylor et al., 2015; Avitabile et al., 2016). But this factor too had little influence on potential carbon losses from overhunting or on total revenue.

The hunting-induced erosion of carbon in tropical forests could be a massive, insidious, and hitherto relatively unappreciated contributor to global climate change. The analyses here present an initial estimate of the factors related to the magnitude of the impacts of local hunting on carbon emissions. The results suggest that enhanced efforts to understand forest responses to cumulative hunting over long time frames (cf. Harrison et al., 2013; Bello et al., 2015; Osuri et al., 2016; Peres et al., 2016), as well as the details of how frugivore ecological function changes with population density, could help alleviate ecosystem-level cascading impacts of hunting. Moreover, these analyses indicate that limiting hunting effort could be in long-term best interests of hunters by precluding the depletion of wild game and foregoing the loss of potential revenue from the sale of forest carbon credits.

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